THE SMALL ENTELODONTS OF THE WHITE RIVER OLIGOCENE.

Investigation aided by a grant from the Marsh Fund of the National Academy of Sciences.

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(*Read April 22, 1922.*)

Contributors to the literature on the entelodonts or so-called "giant pigs" are in agreement in regarding the small animal with closely crowded lower premolars (p_1 excepted) from the Titanotherium beds of the Cypress Hills, Saskatchewan, generally known as *Archæotherium coarctatum* Cope, not only as quite distinct specifically, but also as more primitive than the other American forms, Mr. Troxell in his recent paper even referring it to the European genus *Entelodon.*[1]

The Princeton Expedition of 1921 was so fortunate as to secure from the Oreodon beds the skull and lower jaws of a small entelodont with unspaced lower premolars (the first excepted) and reduced m^3, and a search through our own collections and those of the American Museum of Natural History, kindly placed at my disposal by Professor Osborn and Dr. Matthew, has brought to light additional material which makes it desirable to view the situation somewhat differently from that indicated above.

The recently acquired Princeton specimen (No. 12624, Figs. 1 *A*, 2, 3 *B*, 4 *A*) was found by Mr. H. R. Wanless, to whom we are indebted for the discovery of so many fine entelodont skulls during the last two summers, and is from clays intercalated in the lower zone of rusty nodules in the Lower Oreodon beds at Culbertson's[2] locality on Bear Creek (Princeton collecting locality 1016E2A) about four

[1] E. D. Cope, "Contributions to Canadian Palæontology," Vol. III., pp. 20–21, Pl. XIV., Figs. 3, 3*a*, 1891. O. A. Peterson, *Memoirs Carnegie Museum*, Vol. IV., No. 3, pp. 55–56, Fig. 11, 1909. E. L. Troxell, *American Journal of Science,* Vol. L., p. 249, 1920.

[2] See T. A. Culbertson's diary under date of May 14, 1850, in Fifth Annual Rept. Smithsonian Inst., p. 93.

and one half miles northeast of Scenic, Pennington County, South Dakota, and about a mile south of where "71 Table," the local name for a mesa-like area of high plain, ends. In this specimen all the

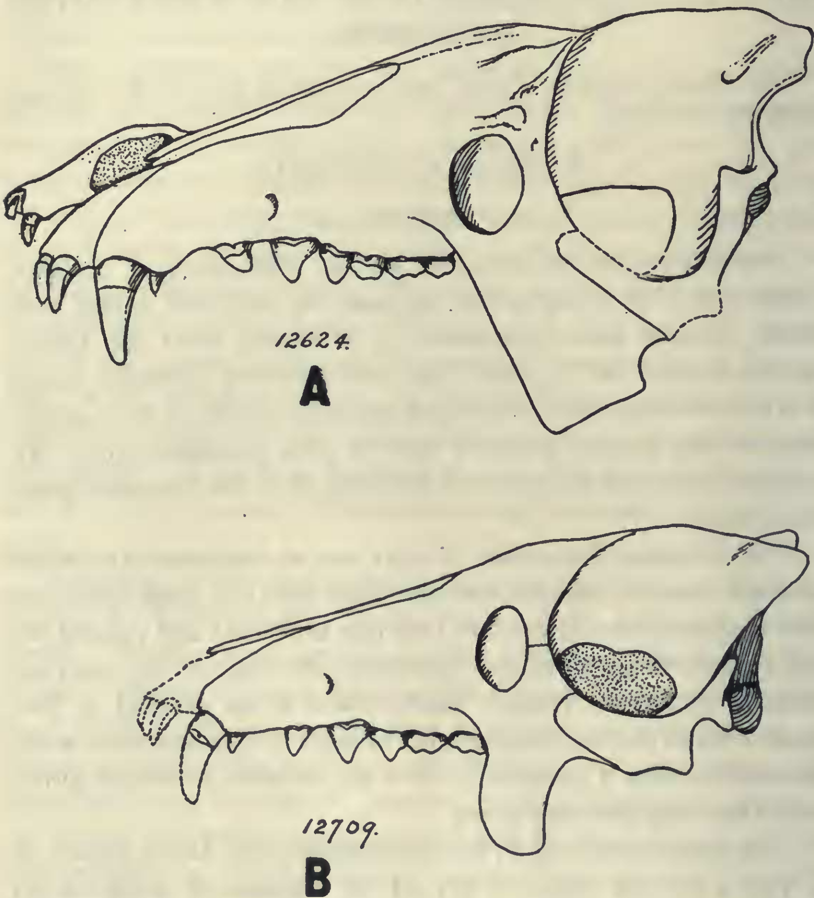
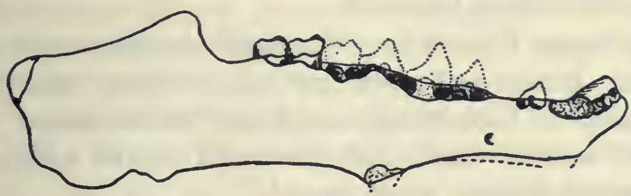


FIG. 1. *A. Archæotherium mortoni,* No. 12624 Princeton University Geological Museum. Left side of slightly distorted skull, about one fifth the natural size; view not in absolute profile. Large size-variant with reduced cuspidation in m^3 and crowded anterior lower premolars. *B. Archæotherium mortoni,* No. 12709 Princeton University Geological Museum. Left side of uncrushed skull, about one fifth natural size; view in absolute profile. Small size-variant with unreduced cuspidation in m^3.

lower teeth except the last two molars had fallen from the jaw previous to fossilization, but the alveoli of the cheek teeth are well preserved and in contact, with the exception of those for the two roots of p_1, which are some 4 mm. removed from the canine alveolus and 14 mm. from the alveolus for the anterior root of p_2. In the upper dentition, where there is no indication of premolar crowding, a very decided simplification in the crown pattern of the third molar is found and a reduction in the size of the tooth as compared with other specimens in which a larger number of cusps are present. In the anterior row (Fig. 3 *A, B,* left m^3) there are two large cusps slightly joined in front by a sharp saddle, with almost no protoconule (Fig. 3 *B*) or, in another specimen, with a small development of this cusp (Fig. 3 *A*). In the posterior row, the metacone is well developed, there is a very small metaconule sometimes not completely differentiated from the former, and a heavy posterior cingulum, which terminates against the protocone without any suggestion of a hypocone. The second Princeton specimen just referred to (No. 12544) showing this type of third molar is also from the lower zone



12624.

FIG. 2. *Archæotherium mortoni,* No. 12624 Princeton University Geological Museum. Right ramus of lower jaw from the outer side, about one fifth natural size. The anterior teeth are indicated by dotted outlines to localize the alveoles.

of rusty nodules of the Lower Oreodon beds, but lacks the lower jaw. In the collection of the American Museum of Natural History a very small skull, No. 1481, from the Oreodon beds on Hat Creek, Nebraska, shows an extreme degree of crowding of the lower anterior premolars (c–p_1, 4 to 5 mm.; p_1–p_2, 2.5 mm. to 3 mm.; p_2–p_3, 3 mm. to contact) associated with a type of m^3 indistinguishable from that just described. In a partial skull without lower jaws in the same collection, from the Middle Titanotherium beds on Lance Creek, Wyoming, the third upper molar (Fig. 5), which here has a slight external cingulum, shows even greater reduction of the cuspidation in the posterior row where the posterior intermediate is absent and metacone and posterior cingulum blend.

It is evident from the above that small forms with reduced m^3, in some of which the lower anterior premolars are closely crowded, have a wide range both in space and time, and it will, accordingly, be advisable to look into the matter of their relationship with both *Archæotherium coarctatum* and *A. mortoni*. All of the specimens to which I have referred are perfectly typical *Archæotherium,* differing from *Entelodon* in the triangular crown and notched anterior border of the fourth upper premolar, the spacing between the upper premolars anterior to p^3, the absence of greater width in the posterior part of the crown of p^3 and the presence of distinct para- and metaconids in the lower molars, where preserved in association with the skull. In view of the comparisons to follow it is a fair presumption that the Cypress Hills form, from its resemblance to the South Dakota and Nebraska skulls in the matter of crowded lower premolar dentition and other features, should properly be referred to *Archæotherium,* rather than to *Entelodon.*

A. coarctatum is based on a left mandibular ramus with all the teeth except incisors and canine, and the following characters are either specified by Cope or may be deduced from his figure.[3] Comparison will be made with the newly discovered material, with crowded lower premolar dentition, as we proceed.

1. *A. coarctatum* differs from all other small entelodonts so far described in the absence of diastemata between the lower premolars, except for a very short one between the first and second, resembling the Bear Creek specimen in this respect, where the diastema is somewhat longer, due to the greater size of the individual and differing from the Hat Creek skull (No. 1481, Am. Mus.) in lacking the small inconstant spacing between p_2 and p_3.

2. The first lower premolar is separated by a very short space from the canine, also true of these specimens.

3. The third premolar is larger than the fourth and the first and second are abruptly smaller than either of the others. P_3 was certainly the largest in the Bear Creek specimen (Princeton 12624), with p_2 not much shorter than p_4, judging from the extent of the empty alveoles. In the skull from Hat Creek the teeth have proportions

[3] Loc. cit., Pl. XIV., Figs. 3, 3*a*.

comparable to those shown in Fig. 4 *B* (see table of measurements) and are slender and compressed laterally.

4. P_1 is said to have a compressed laterally-grooved single root in *A. coarctatum*. There are alveoli for two large roots in No. 12624 (Fig. 4 *A*) and the small p_1 of the Hat Creek specimen is double-rooted.

5. The lower molars of *A. coarctatum* have the anterior tubercles elevated above the posterior row. The same is true in both the Bear Creek and Hat Creek specimens, but not more so than in some individuals of typical *A. mortoni*.

6. Heels in lower molars with three tubercles, the third or posterior median of which is said to be better developed than in *A. mortoni*, especially on the last molar. Cope's figure shows the heel of m_2 to be as wide as the trigonid, with hypoconid and entoconid of the same size, while in m_3 it is narrower, with three large cusps, the hypoconid and entoconid of the same size and the hypoconulid very large. In our Princeton specimen from Bear Creek the heels of both m_2 and m_3 are narrower than the trigonids, with the hypoconid the largest and most prominent of the heel cusps, the other two being distinct but much smaller (Fig. 4 *A*). In the Hat Creek specimen (No. 1481, Am. Mus.) the heel of m_2 is less narrow transversely than in the Princeton specimen, but the hypoconid is still the largest cusp, as it is also in m_3, where the entoconid on the right side is somewhat larger than in the Princeton specimen and of about the same proportions as in it on the opposite side.

7. No internal cingulum is present on the molars of *A. coarctatum* and the enamel is smooth. There are no internal cingula in the specimen from Bear Creek and the enamel is smooth on the triturating surface of the crown and slightly rugose on the sides. In the Hat Creek specimen it is practically smooth.

8. Anterior border of coronoid sloping backward. Notch between coronoid and condyle more deeply concave than in the Bear Creek specimen, where the front edge of the coronoid rises vertically, as it does also in No. 1481 from Hat Creek.

9. Lower premolar crowns strongly compressed laterally, especially the anterior ones. None are preserved with our No. 12624, but

in No. 1481, Am. Mus., they are as strongly compressed laterally as in our No. 11440 (Fig. 4 *B*), a typical *A. mortoni* as noted later.

Certain unassociated upper molars from the Cypress Hills locality are referred to *A. coarctatum* by Cope and Lambe.[4] Of these, the third molar, as figured by Lambe, has three well-developed and subequal cusps in the posterior row and strong external cingulum, quite different from the less complex type of cuspidation found in the specimens just described. Whether this specific reference is correct

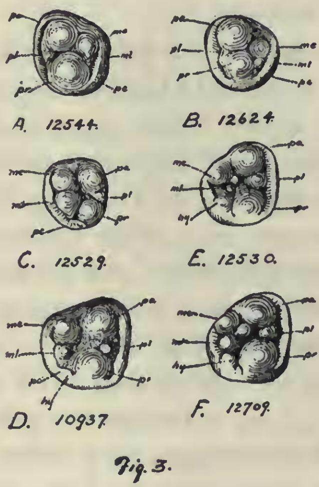


FIG. 3. *Archæotherium mortoni.* Series of crown views, from contemporary animals, of the third upper molar, one half the natural size, showing some of the variations in cusp development. *A* and *B* are of the left side; the others are of the right side. *C* is drawn from a tooth not fully erupted, the anterior cingulum being still covered by bone. *pr,* protocone; *pl,* protoconule; *pa,* paracone; *me,* metacone; *ml,* metaconule; *pr,* posterior cingulum; *hy,* hypocone.

can not be determined until lower jaws of unquestioned *coarctatum* type are found in association with upper molars.

The skulls from Hat Creek and Bear Creek differ greatly in size (see table of measurements) and the latter has been deformed somewhat by crushing, and has, unfortunately, lost the tip of the cheek

[4] L. M. Lambe, "The Vertebrata of the Oligocene of the Cypress Hills, Saskatchewan," *Contributions to Canadian Palæontology,* Vol. III., Part IV., p. 26, Pl. II., Figs. 10, 11, 1908.

flange and the dependent mandibular processes. The outward and backward slope of the cheek flange (Fig. 1 *A*) is undoubtedly accentuated by crushing, but its width has not been increased thereby. Apart from its greater size, the part remaining is not essentially unlike that of the small skull in the American Museum collection (Hat Creek specimen), which, in turn, except for the reduced m^3, can not be distinguished from our No. 12709 shown in Fig. 1 *B* and regarded as typical *A. mortoni*.

The type of *A. coarctatum* lacks the inferior mandibular border anterior to the "first" (fourth) premolar, consequently the shape of the dependent processes is unknown. Both processes are lost by decay in No. 12624 (Fig. 2), but were evidently present. Fortunately, they are well preserved in the Hat Creek specimen (Am. Mus., No. 1481), where they are seen to be of the *A. mortoni* type, made familiar by Peterson's drawing.[5]

Turning now to *A. mortoni*, the type specimen, a fragment of the maxillary with p^3 and p^4 in place, figured by Leidy on Plate IX., Fig. 3, "Ancient Fauna of Nebraska," is manifestly inadequate from the modern point of view, but we must not forget that Leidy was just as fully entitled to find his own original type inadequate as any subsequent writer and, therefore, to redefine it in terms of other specimens. The young individual with milk and permanent dentition which he figures on Plates VIII. and IX. of the Ancient Fauna is, therefore, an "heutotype," as this term is defined by Schuchert and Buckman.[6] On this specimen, I submit, the species *Archæotherium mortoni* is adequately founded. It is an individual with richly tuberculated third upper molar, with three cusps in the front row and a large number of small tubercles in the posterior row among which the metacone, metaconule, hypocone, posterior cingulum and an additional cusp anterior to the metacone and metaconule may be made out, although by no means as distinctly as in Fig. 3 *E* and *F*. There may be departures from this fully tuberculated type of m^3 in the development of the hypocone which may be barely distinguishable from the posterior cingulum (Fig. 3 *D*) or large and fully formed (Fig. 3

[5] Loc. cit., p. 48, Fig. 4.

[6] *Science*, N. S., Vol. 21, No. 545, p. 900, 1905.

E, F), and also a variation in the size of the metaconule (Fig. 3 *C–F*). Lower jaws are associated with some of the skulls showing these types of third molar and in them variations in the spacing of the anterior premolars and in the structure of the lower molar heels

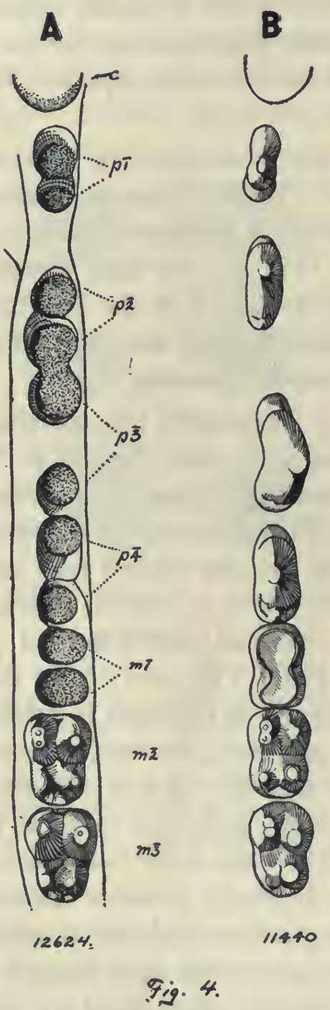


FIG. 4. *Archæotherium mortoni*, lower dentition of the right side crown view, one half of the natural size. *A*. Lower jaw of large skull from Bear Creek, showing the empty alveoles of the anterior teeth, m_2 and m_3 alone remaining in place. *B*. Lower dentition with well-spaced premolars belonging with a small skull from Sand Creek, Nebraska. Both specimens in the Princeton collection.

may be noted. Princeton No. 11440 is a typical *A. mortoni* with a large hypocone on m^3 widely spaced anterior lower premolars and a large hypoconulid and entoconid in the heel of m_3 (Fig. 4 *B*). No. 1483, American Museum, from the Oreodon beds on Hat Creek, Nebraska, has the hypocone of m^3 intermediate in size between that shown in Fig. 3 *D* and 3 *F*, with the spacing between the lower premolars as follows: c–p_1, 5 to 7.5 mm.; p_1–p_2, 11.5 to 13 mm.; p_2–p_3, 3.5 to 4 mm.; p_3–p_4, 2 mm. to contact, in contrast with c–p_1, 6; p_1–p_2, 9; p_2–p_3, 17; p_3–p_4, 3.5, as shown in Fig. 4 *B*. In this second Hat Creek specimen the heel of m_3 is similar to that of our No. 12624 (Fig. 4 *A*), except that the hypoconulid is a broad ledge instead of being broken up into accessory cusps. In Peterson's figure[7] the spacing of the lower premolars is as shown in our Fig. 4 *B*, the hypocone is small and but slightly differentiated from the posterior cingulum in m^3, and the third lower molar has a heel similar to that shown in Fig. 4 *A*, except for the minor cuspidation there seen. The longest gap in lower premolar spacing is ordinarily between p_2 and p_3 as in Fig. 4 *B*, but in No. 1483, American Museum, reference to the dimensions just given will show that it is between p_1 and p_2. All the variations in molar pattern shown in Fig. 3 are strictly contemporaneous, all the specimens being from the lower zone of rusty nodules of the lower Oreodon beds. Whether the development of cingula, rugose enamel and accessory cuspules in the teeth of entelodonts is to any extent nutritionally controlled, as suggested by Nathusius's[8] observations on domesticated pigs, is difficult to determine, but may well be used with caution in establishing or defining species.

We may next turn to the specimens in the Yale collection which Mr. Troxell has named *A. clavus clavus* and *A. clavus darbyi*. Mr. Peterson, in his monograph on *Dinohyus*,[9] has regarded the first as a subspecies of *A. mortoni*, and I have elsewhere indicated my inability to distinguish between them and specimens in the Princeton collection referable to *A. mortoni*. The material secured by our 1921 Expedition rather increases the difficulty in that it presents additional types

[7] Loc. cit., pp. 48, 49, Figs. 4–6.

[8] Vorstudien für Geschichte und Zucht der Hausthiere Zunaechst am Schweineshaedel. H. von Nathusius, Berlin, 1864.

[9] Loc. cit., p. 49.

of molar pattern and premolar spacing in association with skull structures like those of Mr. Troxell's *clavus* and *darbyi,* which, in turn, are not essentially unlike those of *A. mortoni.* An examination of Mr. Troxell's text and Fig. 3[10] will show that m^3 of *A. clavus clavus* is of much the same general type which I have attempted to represent in Fig. 3 *D.* Mr. Troxell describes it as follows: "The protocone has a position midway fore and aft, and has encroached on the hypocone so that the latter is scarcely visible; it is, in fact, smaller than the metaconule and is nothing more than a heel, continuous with the hypostyle. The metacone is also lower than the metaconule, which already shows a lake of dentine by reason of the wear." In the inferior dentition, in m_2 "the hypoconid is strongly developed; on the other hand, the entoconid is weak. A distinct posterior heel may be seen. M_3 is much like m_2, except that a very marked posterior heel and a less strong hypoconid are observed," and these points are well brought out in the drawings accompanying Mr. Troxell's text. In

FIG. 5. *Archæotherium mortoni,* No. 9315 American Museum. Right upper m^3 showing an extreme degree of cusp reduction. One half the natural size.

A. clavus darbyi m^3 is "round or slightly oval, due to the strong lobes of the para- and hypocones. There is a moderate cingulum anterior only and no heel. The protocone is forward of the mid-line. The hypocone is strong." In Fig. 8 of Mr. Troxell's paper, where the lower teeth, with somewhat worn crowns, are represented, there is a weak entoconid on m_2; no hypoconulid is shown on this tooth, while on m_3 there is a very large hypoconid and a posterior and internal ledge from which the remaining cusps do not seem well differentiated. Perhaps this is what Mr. Troxell refers to when he writes of "the absence of heel in m_3" being an unusual feature which distinguishes it "from the other specimens present." Neither of the Yale specimens possess unspaced lower premolars.

In the presence of this melange of characters I am quite unable to separate species on the basis of constant association of constant differences. Certain characters, like the complication of crown pat-

[10] Loc. cit., pp. 364, 365.

tern in m³, may be regarded as progressive, but among contemporary individuals in the series the increments of change appear to fluctuate in an irregular way, certain cusps in less advanced teeth being very large, while in more advanced teeth they may be quite small (compare m¹, Fig. 3 *C, E*), or small in some and large in others (m¹, Fig. 3 *E, F*). Small bodily size is not confined to individuals with less complex m³ or those with the anterior lower premolars unspaced, and these are connected with the more richly cuspidated and fully spaced types by such a transitional form as No. 1483, Am. Mus., where m³ resembles Fig. 3 *D*, and there are very short spaces between the anterior lower premolars. So far as the assumed primitiveness of *A. coarctatum* is concerned, every one of its characters which might be regarded as primitive is possessed in some degree by specimens which differ from it in other respects, as I have tried to show, and we are faced by two alternatives, either the naming of every variant, which results in making practically every specimen a separate species, for almost every one of them shows a new grouping of characters which appear somewhere else in a different association, or the referring of the lot to one species for which the name *A. mortoni* has priority and which seems, as Dr. Matthew has suggested to me in another connection, to be made up of several interbreeding strains, diagrammatically a number of anastomosing lines, which differ by various small unit characters or combinations thereof, transmitted to the individual from the various pure lines which enter into its ancestry. Reference to the accompanying table of measurements will show a considerable range in size, but I am not able to correlate this, as already indicated, with the structural variations noted above.

The situation with regard to these small entelodonts suggests that certain of the structural differences which have been used for the separation of some of the larger forms would be found to intergrade if we had larger series of contemporary specimens, which, unfortunately, do not yet exist in museum collections. If the conclusions reached above are well founded, it may be considered certain that *A. mortoni* ranges down into the Titanotherium beds,[11] but neither it

[11] Peterson reports a number of skulls, portions of skulls and teeth in the Carnegie Museum, collected by himself and others from the Titanotherium beds of Nebraska and South Dakota and agreeing with *A. mortoni* as figured by Leidy. Peterson, loc. cit., p. 47.

nor the genus to which it belongs has yet been reported from the Protoceras-Leptauchenia level.

	Measurements. Oreodon Beds.						Titanotherium Beds.	
	Am. Mus. No. 1481	P. No. 12530	P. No. 11440	P. No. 12709	Am. Mus. No. 1483	P. No. 11529	P. No. 12624	Am. Mus. No. 9315
Skull length, ant. base of canine to condyle (inclusive)	323	334		343	377	378	423	
p^1–m^3, length	147	173	178	183	181	192	185.5	
m^1–m^3, "	59	69	65.5	78	69.5	67+	65	
p_1–m_3, "	160	—	197	—	188	—	200	
m_1–m_3, "	63	—	71	—	74	—	72	
p^4 ant. post.	18.5	19.5	18.5	22	20	22.5	19	18.25
" transverse	18.5	20	19	22	22.5	21.3	19.5	20
m^1 ant. post.	21	22	20.5	23	21	24	21.25	19
" transverse	22	21	20	23	24±	23	19	19
m^2 ant. post.	21	23	23.5	26.5	23.5	26	23	22.5
" transverse	23.5	23.5	23	25	—	28	22	21
m^3 ant. post.	18	21	21	23	23		18 18.5	17 18
" transverse	18.5	20.5	21	22	24			
m_1 ant. post.	20		22		22			
" transverse	14.5		13		15			
m_2 ant. post.	21.75		23.5		26			
" transverse	16		16		—			
m_3 ant. post.	21.75		24.5		25.5			
" transverse	16.5		15.5		19			

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